TAXONOMIC CLARIFICATION OF *ATRIPLEX NUTTALLII* (CHENOPODIACEAE) AND ITS NEAR RELATIVES

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ABSTRACT

In 1874 Sereno Watson described *Atriplex nuttallii* as a new species, citing his number 981 collection, made in 1868 from northern Nevada, as a representative. His collection consisted of three plants each collected from a separate population all mounted on one sheet. One is *A. canescens*, two are the new species, *A. nuttallii*. Failure to recognize the original collection and collection site of *A. nuttallii* has resulted in assignment of the name *A. nuttallii* to several different *Atriplex* species in western North America. However, by using quantitative as well as qualitative differences, *A. nuttallii* is readily distinguished from its near relatives *A. cuneata*, *A. falcata*, *A. gardneri*, and *A. tridentata*. The principal distinguishing features include plant size and habit, leaf dimensions, fruiting-bract size and shape, fruiting bract appendages, chromosome number, saponin content, flavonol content, dates of anthesis, and geographic distribution.

RESUMEN

En 1874 Sereno Watson describió *Atriplex nuttallii* como nueva especie, citando su recolección número 981, hecha en el norte del estado de Nevada, E.E.U.U., como representativa. Consiste esta recolección en tres plantas, de distintos lugares pero colocadas todas en un mismo pliego de herbario. Una de ellas es *A. canescens* y dos son de la nueva especie, *A. nuttalli*. El no darse cuenta los botánicos de la colecta original y su lugar de origen ha tenido como consecuencia la aplicación del nombre de *Atriplex nuttallii* a varias otras especies de *Atriplex* del oeste de Norte América. Sin embargo, usando tanto características cuantitativas como cualitativas, se distingue fácilmente *A. nuttallii* de las especies afines, *A. cuneata*, *A. falcata*, *A. gardneri*, y *A. tridentata*. Las características de mayor utilidad son la altura de la planta, las dimensiones de la hoja, la forma y tamaño de las brácteas fructíferas, sus apéndices, el numero de cromosomas, contenido de saponinas, contenido de flavonoides, fecha de antesis, y la distribución geográfica.

INTRODUCTION

In 1874, Sereno Watson described *Atriplex nuttallii* as new (Watson 1874) and listed his collection number 981, obtained in 1868 in northern Nevada, as a representative of the species. This collection consists of three plants

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collected at different times in separate locations in northern Nevada, all mounted on one herbarium sheet (GH!) (Fig. 1), and each labeled by Watson as *Obione canescens* Moq. The plant on the right is *A. canescens* (Pursh) Nutt. collected in June, 1868, in Unionville Valley, Pershing County, Nevada. The other two are *A. nuttallii*. The middle plant, which appears to have been broken and folded back, was collected in September, 1868, in Thousand Springs Valley, Elko County, Nevada. The plant on the left was collected in July 1868 in Reese Valley, Lander County, Nevada. Currently there are still extensive populations of these species in the valleys where Watson collected them.

As shown in Figure 1, several botanists have recognized differences between these three plants and have provided annotations for them. In 1951, Grant D. Brown annotated the plant on the right as *Atriplex canescens* (Pursh) Nutt. In 1962, C.A. Hanson annotated the plants on the left and right as *Atriplex bonnevillensis* Hanson and the central one as *Atriplex falcata* (Jones) Standley. In 1972, I.J. Bassett and C.W. Crompton annotated the plant on the right as *Atriplex canescens*, the central one as *A. nuttallii* var. *falcata*, and designated on the annotation label, the left specimen as the lectotype of *Atriplex nuttallii* S. Watson. Later, McNeil et al. (1983) designated as the lectotype of *A. nuttallii*, a specimen collected in Saskatchewan, Canada, by Bourgeau (*s.n.*), in 1857, and included by Watson among 10 other collectors of *A. nuttallii*, in addition to *Watson 981*. However, as directed in the International Code of Botanical Nomenclature, Article 9.9 (Greuter et al. 1994), — " when the material designated as type is found to belong to more than one taxon, a lectotype — may be designated," and, as described in Article 7.5 of the 1988 edition of the code (Greuter et al. 1988), "A lectotype is a specimen or illustration selected from the original material to serve as a nomenclatural type when no holotype was designated at the time of publication —. When two or more specimens have been designated as types by the author ... the lectotype must be chosen from among them." Since Watson listed in the protologue, his number 981 as a representative of the new species, he ostensibly considered it typical and, since this collection consists of three specimens, one of them must be chosen as the lectotype. Consequently, the lectotype of *Atriplex nuttallii* is the specimen on the left (GH) as annotated by Bassett and Crompton in 1972. The designation by McNeil et al. of a specimen collected in Saskatchewan, Canada as the lectotype of *A. nuttallii*, was therefore unnecessary. The illustration in Bassett et al. (1983) of the Saskatchewan plants, is representative of a diploid *A. gardneri* (Moquin-Tandon) Hall & Clements which is common throughout southern Alberta, southern Saskatchewan and northern Montana but very different from *A. nuttallii* of northern Nevada. In his protologue, Watson de-

FIG. 1. *Atriplex nuttallii*. The lectotype of *Atriplex nuttallii* (*Watson 981*, upper left corner) collected in Reese Valley, Lander County, Nevada, July 1868. The central element is *A. nuttallii* collected in Thousand Springs Valley, Elko County, Nevada, September, 1868. The specimen on the right is *Atriplex canescens* collected in Unionville Valley, Pershing County, Nevada, June 1868.

scribes *A. nuttallii* as being 1–2 feet high. This is the stature of the *A. nuttallii* plants in the populations he collected in northern Nevada (Table 1) but not *A. gardneri* plants which are mostly 6–12 inches tall, nor *A. canescens* plants which are seldom less than 30 inches in height. The Saskatchewan plant illustrated in Bassett et al. (1983) appears to be ca 12 inches in height.

In the botany treatment of the King expedition (Watson 1871), Torrey provided identification for Watson's collections and Watson provided the descriptions (footnote, page 287). Referring to *Watson 981*, Torrey identified it as *Obione canescens* Moq. and Watson applied that name to each of the three plants. Watson's description of the collection specifically referred to his number 981 and indicated that "most of the specimens have nearly or quite wingless fruit. Others have the bracts considerably dilated, though still less than is frequently the case (982)," indicating that he recognized it as being anomalous, quite unlike other *Obione* (*Atriplex*) *canescens* plants. As shown in Figure 2, there is considerable variation in the fruiting-bract characteristics of plants in the Reese Valley population, with none being truly 4-winged.

Since Watson, following Torrey's identification, labelled each of the three specimens (*Watson 981*), *Obione canescens*, he apparently assumed the variation he saw in the populations in northern Nevada to be representative of the variation displayed by *Atriplex* shrubs throughout western United States. This is confirmed in his later description of *A. nuttallii* (Watson 1874) wherein he lists *Atriplex canescens* Nuttall, not of James, *Obione canescens* Moq., and *Atriplex Gordoni* Hook. as synonyms and gives its distribution as "from the Saskatchewan to Colorado and Northern Nevada."

This broad interpretation by Watson appears to have been the initiation of a series of misconceptions concerning the geographic distribution of *A. nuttallii* that we interpret to be confined to northern Nevada and northwestern Utah (Fig. 3). Standley (1916) listed the type locality of *A. nuttallii* as "on the denuded hills of the Missouri River, about 15 miles below the confluence of the White River, South Dakota." Since this is the location given by Nuttall (1818) as the type locality of *Atriplex canescens* (Pursh) Nutt., Standley clearly confused the two. Furthermore, this locality for *Atriplex canescens* (*Calligonum canescens* Pursh) invites correction because its origin given by Pursh (1814) is "in the plains of the Missouri River, near the Big Bend" which is several kilometers upstream from the confluence of the White River.

Standley (1916) also mistakenly listed the distribution of *A. nuttallii* as "alkaline plains and hillsides, Manitoba and Saskatchewan to northern Utah, Colorado and western Nebraska" without mentioning Reese Valley and Thousand Springs Valley in northern Nevada.

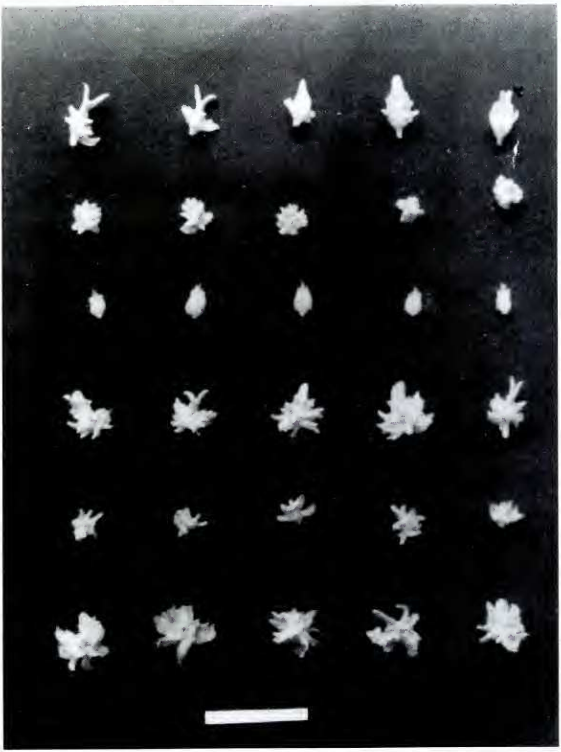

FIG. 2. Fruiting-bracts of six randomly selected plants of *Atriplex nuttallii* from a population in Reese Valley, ca 1 km west of Battle Mountain, Lander Co., Nevada. Each row across represents one individual. Bar = 15 mm.

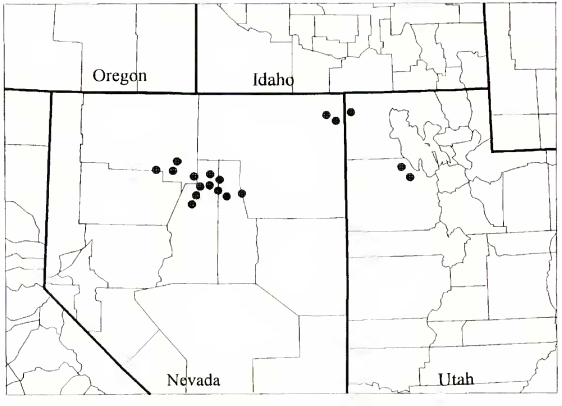

FIG. 3. Distribution of known populations of *Atriplex nuttallii*.

Hall and Clements (1923) likewise failed to include the type locality of *A. nuttallii* in their description of the distribution of *A. nuttallii* as "Saskatchewan and South Dakota to western Nebraska, New Mexico, Arizona, northwestern California, eastern Washington, and Alberta."

Recently, Basset et al. (1983) cited the distribution of *A. nuttallii* as "from the Peace River District of Alberta to Manitoba. In the United States specimens have been found as far south as Colorado." Clearly this does not refer to the *A. nuttallii* described by Watson from Nevada.

The failure to identify the original collection site of *A. nuttallii* in all references has caused considerable misunderstanding of its identity and has resulted in the assignment of this binomial to most of the suffrutescent shrub species of *Atriplex* in western North America. Ulbricht (1934) listed *A. nuttallii* S. Wats., *A. buxifolia* Rydb., *A. cuneata* A. Nelson, *A. eremicola* Osterh., *A. falcata* Standley, *A. gordonii* Hook., *A. neomexicana* Standley, *A. oblanceolata* Rydb., *A. pabularis* A. Nelson and *A. tridentata* Kuntze as synonyms of *Obione gardneri* Moq. (*Atriplex gardneri* [Moq.] Standley). Hall and Clements (1923) treat *A. buxifolia*, *A. cuneata*, *A. eremicola*, *A. falcata*, *A. gardneri*, *A. pabularis* and *A. tridentata* as subspecies of *nuttallii*.

Standley (1916) listed eight species as close relatives of *A. nuttallii* (Series Nuttallianae): *A. buxifolia*, *A. cuneata*, *A. falcata*, *A. gardneri*, *A. neomexicana*, *A. oblanceolata*, *A. pringlei* Standley, and *A. tridentata*. As suggested by Hall

and Clements (1923), *A. pringlei* appears to be an insignificant variant of *A. acanthocarpa* (Torr.) S. Wats and *A. oblanceolata* is non-distinguishable from *A. gardneri*. *A. neomexicana* is a common reoccurring hybrid between *A. cuneata* and *A. confertifolia* (Torr. & Frem.) S. Wats. (Hanson 1962) and *A. buxifolia* is synonymous with *A. gardneri*. The remaining four species, *A. cuneata*, *A. falcata*, *A. gardneri*, and *A. tridentata*, were treated by Hall and Clements (1923) as subspecies of *A. nuttallii*. Since they and *A. nuttallii* are clearly distinct phenotypically (Pope 1976, Tables 1, 2, Fig. 4) and geographically (Figs. 3, 5–8) we consider them best treated as separate species as proposed by Standley (1916).

Because Watson listed *A. gordoni* (*A. gardneri*) as a synonym of *A. nuttallii*, Hanson (1962) argued that the epithet *nuttallii* was superfluous and hence illegitimate and that *A. gardneri* was the correct name for Watson's *A. nuttallii*. This view was later accepted by Pope (1976) Stutz (1978), Stutz et al. (1979), and Welsh (1984). However, as noted by McNeil et al. (1983), the listing of *A. gordoni* (*A. gardneri*) as a synonym of *A. nuttallii* was accompanied by a question mark and is therefore not a legitimate synonym and, according to the Code, Article 55.2, note 1, (Greuter et al. 1994) the epithet *nuttallii* is therefore not nomenclaturally superfluous.

As discussed by McNeil et al. (1983) the other synonyms of *A. nuttallii* listed by Watson: (*Atriplex canescens* Nuttall, and *Obione canescens* Moq.), are also not legitimate synonyms.

MATERIALS AND METHODS

To better define *A. nuttallii* and its near relatives, herbarium specimens of the suffrutescent *Atriplex* species of western North America were examined in several herbaria (BRY, CAS, GH, MO, NY, PH, RM, RSA, US, UC) and specimens were collected and studied from the original collection sites of each of the species included in the study (except *A. gardneri* for which the exact location is not known). In addition, morphological measurements, saponin production, flavonoid content, and cytological studies were made of plants in several populations of each species. The morphological measurements included fruiting-bract characteristics, plant height and width, and leaf length and width. Chromosome counts were obtained from plants in several populations of each species (Figs. 5–8). In some cases the counts were obtained from root tips squashed in aceto-carmine stain, but most were from aceto-carmine squashes of pollen-mother-cells derived from anthers fixed in 5% acetic acid and stored under refrigeration. Saponin content was determined by hemolysis of red blood-cells as described by Sanderson et al. (1987). Flavonoid content was determined by paper chromatography as described by Sanderson and Stutz (1984).

TABLE 1. Plant and leaf characteristics of *Atriplex nuttallii* and its near relatives. Measurements were obtained from 20 plants in each population. Diploid *A. cuneata* is not included because of extensive between-population variation. N = number of populations. Data = mean with coefficient of variation in parentheses. Values in each column with the same letter are not significantly different ($p<.05$).

		Plant			Leaf		
Taxon	N	Height (cm)	Width (cm)[a]	Volume (dm^3)[b]	Length (mm)	Width (mm)	l/w
A. nuttallii(6x)	9	32.6(0.41)^{A}	47.4(0.39)^{A}	101.5(0.94)^{A}	24.1(0.33)^{A}	4.0(0.21)^{B}	6.0(0.22)^{A}
A. cuneata(4x)	31	12.8(0.31)^{B}	51.2(0.33)^{A}	41.3(0.88)^{AB}	20.9(0.22)^{A}	8.3(0.28)^{A}	2.6(0.19)^{BC}
A. falcata(2x)	12	12.9(0.44)^{B}	24.6(0.31)^{B}	9.4(0.74)^{B}	23.7(0.58)^{A}	3.6(0.41)^{B}	6.5(0.23)^{A}
A. gardneri(2x)	6	9.8(0.52)^{B}	48.9(0.11)^{AB}	25.2(0.76)^{AB}	19.9(0.09)^{A}	3.8(0.21)^{B}	5.4(0.11)^{AD}
A. gardneri(4x)	8	10.9(0.59)^{B}	49.8(0.44)^{A}	42.3(1.45)^{AB}	19.4(0.19)^{A}	5.3(0.28)^{B}	3.8(0.18)^{BCD}
A. tridentata(6x)	13	23.9(0.38)^{A}	41.8(0.46)^{AB}	63.8(1.25)^{AB}	28.7(0.53)^{A}	4.1(0.33)^{B}	6.79(0.28)^{A}

[a] Width of *A. tridentata* does not include root sprouts.
[b] Volume = height × $(\text{width})^2$

Table 2. Fruiting-bract characteristics of *Atriplex nuttallii* and its near relatives. Measurements were made on 20 fruits from several randomly selected plants in each sampled population. Diploid *A. cuneata* is not included because of extensive between-population variation. N = number of populations. Data = mean with coefficient of variation in parentheses. Values in each column with the same letter are not significantly different ($p<.05$).

		Fruiting-bract						
Taxon	N	Length (mm)	Width (mm)	l/w	Volume (mm^2)[a]	Apex[b]	No. of Terminal Teeth	Appendages[c]
A. nuttallii(6x)	10	$4.5(0.10)^{B}$	$3.0(0.07)^{BCD}$	$1.6(0.14)^{AB}$	$39.0(0.15)^{B}$	$2.4(0.07)^{B}$	$3.2(0.24)^{B}$	$2.0(0.14)^{B}$
A. cuneata(4x)	15	$6.1(0.16)^{A}$	$5.0(0.22)^{A}$	$1.3(0.14)^{C}$	$165.3(0.59)^{A}$	$1.8(0.19)^{C}$	$3.6(0.24)^{B}$	$3.9(0.17)^{A}$
A. falcata(2x)	12	$4.6(0.19)^{B}$	$2.6(0.14)^{D}$	$1.8(0.10)^{A}$	$32.0(0.48)^{B}$	$3.0(0.00)^{A}$	$1.0(0.00)^{C}$	$2.0(0.27)^{B}$
A. gardneri(2x)	7	$3.1(0.14)^{C}$	$2.5(0.21)^{D}$	$1.3(0.17)^{BC}$	$19.7(0.45)^{B}$	$1.7(0.19)^{C}$	$4.64(0.46)^{B}$	$1.4(0.19)^{B}$
A. gardneri(4x)	10	$4.2(0.21)^{BC}$	$3.0(0.31)^{BCD}$	$1.5(0.12)^{BC}$	$45.1(1.12)^{B}$	$1.5(0.05)^{C}$	$3.8(0.12)^{B}$	$1.9(0.37)^{B}$
A. tridentata(6x)	13	$4.6(0.12)^{B}$	$3.9(0.16)^{BC}$	$1.2(0.15)^{C}$	$72.6(0.39)^{B}$	$2.6(0.15)^{B}$	$8.5(0.45)^{A}$	$2.0(0.49)^{B}$

[a] Volume = length × $(\text{width})^2$.

[b] Prominence of central apical tooth was scored 0 to 3 with central tooth absent = 0, small = 1, conspicuous = 2, prominent = 3.

[c] Number of lateral appendages was scored 0 to 5 with no appendages = 0, numerous appendages = 5.

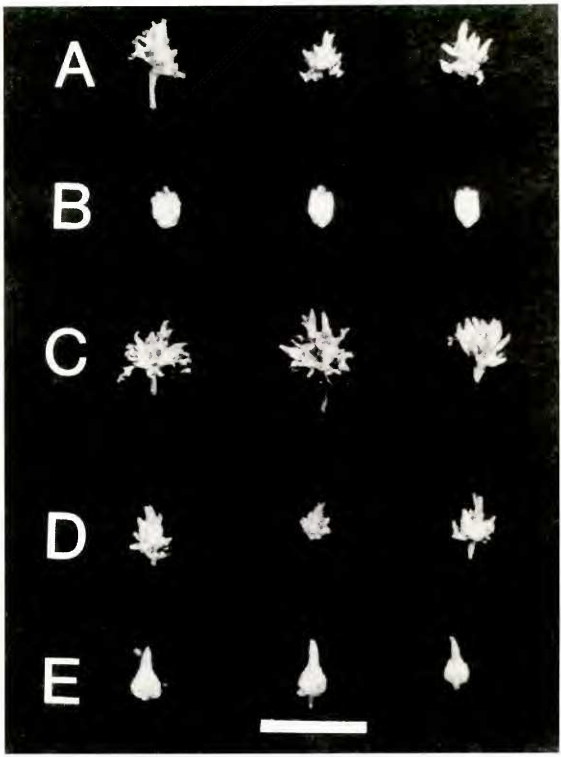

FIG. 4. Fruiting bracts of *Atriplex nuttallii* and its near relatives. A, *A. nuttallii*. B, *A. tridentata*. C, *A. cuneata*. D, *A. gardneri*. E, *A. falcata*. Although there is considerable variation in the fruiting bracts of plants within and between populations, those shown are fairly representative of each species. Collection sites for those shown are: *A. nuttallii*, 1 km W of Battle Mountain, Lander Co.: Nevada; *A. tridentata*, Rush Valley, Tooele Co.: Utah; *A. cuneata*, Navajo Mine lease site, ca 10 km SW of Farmington, San Juan Co.: New Mexico; *A. gardneri*, ca 10 km S of Bridger, Uinta Co.: Wyoming; *A. falcata*, ca 5 km N of Ontario, Malheur Co.: Oregon. Bar = 15 mm.

RESULTS AND DISCUSSION

Probably because they are dioecious and wind-pollinated, most of the shrubby species of *Atriplex* in North America are unusually rich genetically and can often be best defined by quantitative, in addition to available qualitative, attributes. This is particularly true for *A. nuttallii* and its relatives. As shown in Figures 3, 5–8 and Tables 1–4, although *A. nuttallii* and each of its near relatives can usually be distinguished from each other by some qualitative differences, when combined with differences in quantitative attributes and geographic distributions, they are quite distinct.

Atriplex nuttallii S. Watson, Proc. Amer. Acad. Arts 9:116.1874. LECTOTYPE: NEVADA: Reese Valley, Jul 1868, *Watson 981* (GH!).

Phenotypically, *A. nuttallii* appears to be most closely related to *A. tridentata*. Although highly variable in *A. nuttallii* (Fig. 2), most fruiting bracts of both taxa have multiple, terminal, marginal teeth. Both have oblong or oblanceolate leaves and occupy similar habitats (primarily saline bottomlands). Both are hexaploids ($2n=54$) (a few tetraploid populations of *A. tridentata* have also been found). *A. nuttallii* differs from *A. tridentata* in being taller statured (30–60 cm vs 10–30 cm) (Table 1), woodier, and more phenotypically variable. Much of its variation appears to be the result of hybridization and subsequent introgression from other species, including *A. tridentata* with which it is often sympatric. Plants of *A. tridentata* do not produce saponins whereas some plants of *A. nuttallii* do, some do not (Table 3). *A. tridentata* usually shows aggressive root-sprouting whereas *A. nuttallii* is distinctly caespitose with numerous (60–120), slender (1–3 mm in diameter), woody stems emerging from a single woody crown, 10–50 cm in diameter. Geographically, *A. tridentata* is common in northern Utah, southwestern Wyoming, northwestern Colorado and northeastern Nevada (Fig. 8); *A. nuttallii* appears to be restricted to the alkaline valleys in northern Nevada and northwestern Utah (Fig. 3).

Atriplex cuneata A. Nelson, Bot. Gaz. 34:357.1902. TYPE: UTAH. EMERY CO.: Emery, alt. 7,000 ft, 1894, *M.E. Jones 5443* (HOLOTYPE: US!; ISOTYPES: MO! NY! RSA!).

Atriplex oblanceolata Rydb., Bull. Torrey Bot. Club 31:403. 1904. TYPE: COLORADO: Delta, 3 Sep 1897, *J.H. Cowen 4071* (HOLOTYPE: US!; ISOTYPE: GH!).

Populations of *A. cuneata* are restricted primarily to eastern Utah, western Colorado and northwestern New Mexico (Fig. 5). In many places they constitute the dominant vegetation on thousands of acres. The common name of *A. cuneata*, "Castle-Valley clover," connotes its value as a range plant, partly because it is both palatable and nutritious for livestock and wildlife and partly because, were it not there, there would apparently be nothing at all,

TABLE 3. Cytology, saponin production, flavonoid production, and geographic distribution of *Atriplex nuttallii* and its near relatives. The number of plants examined is in parenthesis.

Taxon	2*n*	Saponins	Flavonols		Geographic Distribution	Date of
	Chrom. #	s	6-MeO	3-MeO		Anthesis
A. nuttallii	54 (11)	+,- (11)	+	- (21)	valleys in n NV and nw UT	Jun–Jul
A. cuneata	36 (126)	- (69)	+	- (43)	e UT, w CO, nw NM	Apr–May
A. cuneata	18(87)	-(72)	-	+(62)	e UT, w CO, nw NM	Apr–May
A. falcata	18 (115)	+ (74)	-	+,- (66)	s ID, n UT, sw WY, n NV, s OR, nw CA	May–Jun
A. gardneri	18 (183)	+,- (32)	-	+ (31)	MT, WY, AB, SK	May–Jun
A. gardneri	36 (250)	+,- (63)	+	- (40)	MT, WY, AB, SK	May–Jun
A. tridentata	54 (257)	- (111)	+	- (105)	n UT, n NV, s WY, s ID, nw CO	Jul–Aug

TABLE 4. Key to *Atriplex nuttallii* and its near relatives [Series Nuttallianae of Standley (1916) consisting of species in which the plants are low-statured (less than 6 dm), suffrutescent, perennial, dioecious, shrubs. Leaves are densely furfuraceous, alternate, entire, with Kranz-type anatomy. Fruiting bracts are 2—6 mm long, 2—5 mm broad, usually longer than broad and usually appendaged.]

1. Leaves linear, length more than 5 times the width
   2. Root-sprouting extensive—*A. tridentata*
   2. Root-sprouting none or minimal
      3. Stems 50 or more from a woody crown, each 30—80 cm long—*A. nuttallii*
      3. Stems single or few, each less than 30 cm long—*A. falcata*
1. Leaves ovate to oblong, length less than 5 times the width
   2. Fruiting bracts globose, 3–5 mm long with numerous flattened appendages—*A. cuneata*
   2. Fruiting bracts elliptical to ovoid, 1–3 mm long with few appendages—*A. gardneri*

of forage value. This is conspicuous in many places where populations of *A. cuneata* terminate abruptly against clay slopes that are completely devoid of vegetation. It is also evident in sites where populations of *A. cuneata* have experienced large-scale "die-back" and remain empty until repopulated by new *A. cuneata* plants.

Atriplex cuneata is mostly tetraploid but throughout its range there are several morphologically distinct diploid populations (Fig. 5). The variation present in disjunct populations of tetraploid *A. cuneata* is probably the result of introgression from these diploids, or in some cases, tetraploid *A. cuneata* may have originated polyphyletically from different diploid ancestors.

Atriplex cuneata plants are mostly caespitose and erect with no evidence of root-sprouting or layering. Their fruiting-bracts are usually much larger than the fruiting bracts of *A. gardneri* (Table 2) and are covered with numerous lateral appendages (Table 2, Fig. 4). They are usually free of saponins, with exceptions only in populations in which introgressive hybridization from other species is suspected. Tetraploid *A. cuneata* plants test positively for the presence of 6-methoxy flavonols and negatively for the presence of 3-methoxy flavonals. In contrast, diploid *A. cuneata* plants test negatively for the presence of 6-methoxy flavonols and positively for the presence of 3-methoxy flavonols (Table 3).

Atriplex falcata (M.E. Jones) Standley, N. Amer. Fl. 21:68. 1916. TYPE: IDAHO. WASHINGTON CO.: Weiser, alt. 2,000 ft, 7 Jul 1899, *M.E. Jones s.n.* (HOLOTYPE: RSA!; ISOTYPE: UC!).

Populations of *A. falcata* are sporadically common in southern Oregon, northeastern California, northern Nevada, northern Utah, southwestern Wyoming and southern Idaho (Fig. 6). It is mostly diploid ($2n=18$), but occasional tetraploid populations occur (Pope 1976).

Phenotypically, *A. falcata* is most easily recognized by its small stature (ca. 13 cm tall × 25 cm broad), small, linear leaves (ca. 24 mm long × 4 mm wide), and small fruiting bracts (ca. 4.5 mm long × 2.5 mm wide),

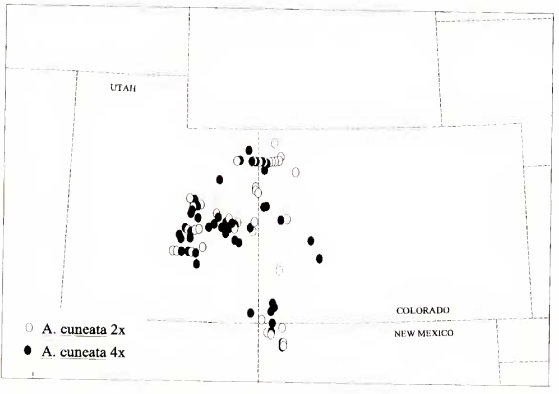

FIG. 5. Geographic distribution of chromosome counts of plants of diploid ($2n=18$) and tetraploid ($2n=36$) *Atriplex cuneata*.

usually without appendages, and terminating in a distinct, acute, central apex (Tables 1, 2, Fig. 4).

The leaves of *A. falcata* produce abundant saponins (Table 3), a trait that can be useful in field identification either by blowing bubbles in a water emulsion of leaves or by tasting a leaf as it is chewed. When saponins are present, bubbles form readily in a leaf-emulsion and the leaves have a distinctly bitter taste. Both of these tests are positive for *A. falcata* leaves, negative for leaves of *A. tridentata* plants with which *A. falcata* plants are sometimes confused. *A. falcata* plants are also readily distinguished from *A. tridentata* plants by their rooting habit: *A. tridentata* plants are vigorous root-sprouters, whereas *A. falcata* plants are caespitose with a single prominent taproot. Also, *A. falcata* plants produce flowers and fruits early in the spring (May–June) whereas *A. tridentata* plants flower and set fruit mostly in mid to late summer (July–August) (Table 3).

Atriplex gardneri (Moq.) Standley, N. Amer. Fl. 21:66. 1916. TYPE: [State?]. La Platte River [date?], *Gordon 250* (HOLOTYPE: GH!, fragments).

Obione gardneri Moq. in DC, Prod. 13:114. 1849.

Populations of *A. gardneri* (2x, 4x) dominate thousands of acres of clay slopes and swales throughout much of southern and eastern Wyoming, central and eastern Montana, western North and South Dakota, southern Alberta,

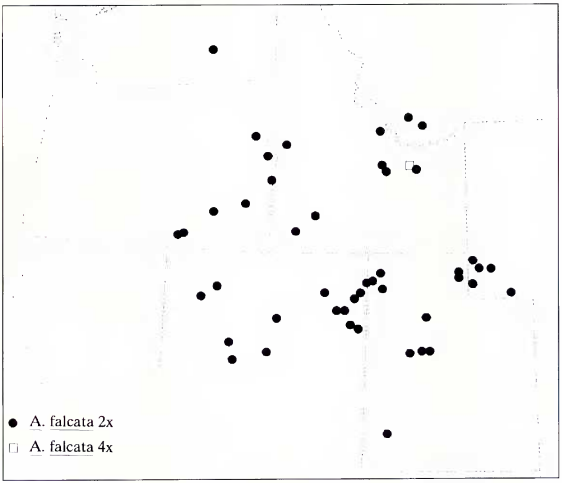

FIG. 6. Geographic distribution of chromosome counts of plants of diploid ($2n=18$) and tetraploid ($2n=36$) *Atriplex falcata*.

and southern Saskatchewan (Fig. 7). Most populations are tetraploid but diploid ones are common. In southern Alberta, southern Saskatchewan and north-central Montana, diploid plants can usually be distinguished from tetraploid plants by their smaller stature, smaller, thinner leaves, finer-textured, less woody stems and smaller fruiting bracts. However, throughout most of the saline deserts of Wyoming and southern Montana, diploid and tetraploid plants are phenotypically very similar although both show considerable phenotypic variation both within and between populations. Chromosome counts of plants in populations bordering Interstate Highway 80 in southern Wyoming, showed a preponderance of tetraploids west of the Continental Divide and a preponderance of diploids to the east (Fig. 9). However, no conspicuous ecological differences were evident between the sites occupied by tetraploids and diploids, nor was it possible to consistently distinguish diploids from tetraploids, phenotypically. This was true for plants in natural populations as well as garden-grown specimens. They are, however, clearly distinguishable by flavonoid differences: tetraploids

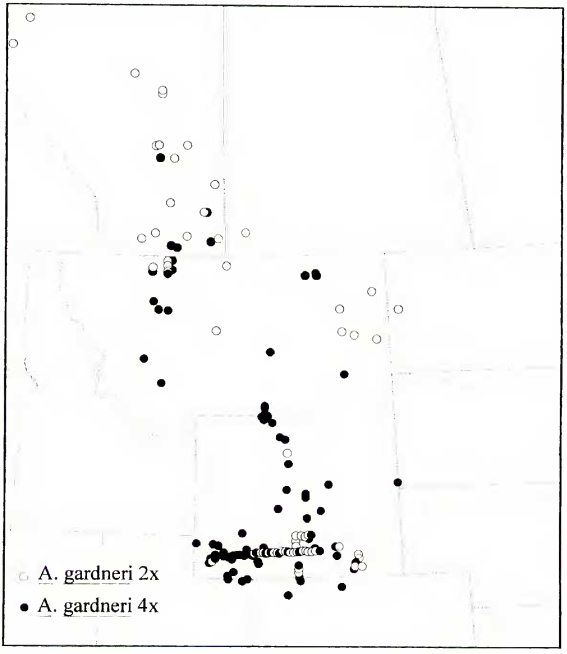

FIG. 7. Geographic distribution of chromosome counts of plants of diploid ($2n=18$) and tetraploid ($2n=36$) *Atriplex gardneri*.

always produce 6-methoxy flavonols, diploids do not; diploids produce 3-methoxy flavonols, tetraploids do not (Table 3). Although both diploids and tetraploids sporadically produce saponins (Table 3), diploids are most often heavy producers, tetraploids usually produce little or none.

Atriplex gardneri plants are short-statured, mostly 4–10 cm in height, (Table 1), but are often more than 80 cm in diameter. The plants are caespitose, arising from a single deep taproot but often show considerable layering. Their fruiting-bracts are usually smaller (ca. 3–4 mm) and have fewer lateral appendages than those of most near relatives (Table 2, Fig. 4).

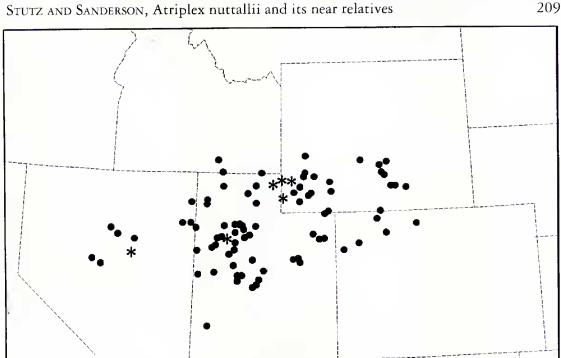

FIG. 8. Geographic distribution of chromosome counts of plants of tetraploid ($2n=36$) and hexaploid ($2n=54$) *Atriplex tridentata*.

Atriplex tridentata Kuntze, Revis. Gen. Pl. 2:546. 1891. TYPE: UTAH: Corinne, 1874, *D.E.O. Kuntze 3084* (HOLOTYPE: NY!).

Two chromosome races of *Atriplex tridentata* have been found: tetraploid ($2n=36$) and hexaploid ($2n=54$). Hexaploids are, by far, the most common, occurring throughout much of western United States and in most of the valley bottoms in Utah and Nevada that were recently occupied by Pleistocene lakes (Fig.8). Only three major tetraploid populations are known: one in Juab County, Utah, one in Eureka County, Nevada, and one in Lincoln County, southwestern Wyoming (Fig. 8). Although tetraploid and hexaploid *A. tridentata* are to some extent, morphologically distinct, the differences do not appear to be sufficient to warrant designation as separate taxa.

Atriplex tridentata differs from other *Atriplex* species in several features, including linear to oblong, furfuraceous leaves, fruiting bracts with conspicuous terminal, marginal teeth (Fig. 4), late-flowering habit (July-August), and vigorous root-sprouting. *A. tridentata* plants are mostly herbaceous above ground with a few slender stems growing erect from woody underground crowns and roots.

The extent of root-sprouting in *A. tridentata* plants is often made conspicuous by its dioecious flowering habit. By noting its flowers, the extent of a single male or single female plant may be easily determined. In some cases individual plants have been found to occupy more than 200 m^2. Sometimes

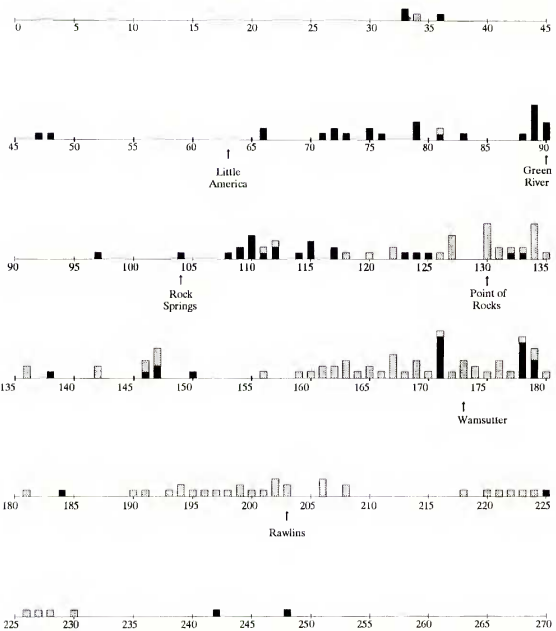

FIG. 9. Distribution of diploid and tetraploid populations of *Atriplex gardneri* alongside Interstate highway 80 in southern Wyoming from the Utah border (mile 0) to near Elk Mountain Wyoming. Chromosome counts were made on plants at each mile marker, when available. Stippled bars = diploids, black bars = terraploids.

a single plant forms a complete carpet in which there are no other plants; at other times the root-sprouting carries a plant around and between plants of other species.

Possibly because of its low saponin content (Table 3), its root-sprouting habit and predominantly herbaceous tissues, *A. tridentata* is often regarded favorably by ranchers as forage for livestock (personal reports).

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